EFFICIENCY OF LIGHT ENERGY CONVERSION IN PLANT GROWTH [1]

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It is 20 years ago that Robert Emerson and C. M. Lewis (5) published an outstanding article on the quantum efficiency of photosynthesis. This study showed that Warburg's at that time unsurpassed high value of this efficiency—only 4 quanta required per molecule of CO_2 reduced—could be reproduced, and even improved. At the same time, however, doubt was thrown upon the tacit assumption that the data obtained were representative for true photosynthesis, by showing that the outcome depended strongly on exactly how the data were evaluated.

This paper opened a new era which led to a much wider understanding of the problem, and to a much increased interest in the detailed techniques of the measurements. In the years thereafter, Emerson, on various occasions, has insisted on the importance of the latter point. A general opinion has gradually developed that the efficiency of true, positive, photosynthesis in the majority of cases is not much better than 1 molecule CO_2 for about 10 light quanta absorbed; however, not all the questions which were raised in the various laboratories, and the merits and shortcomings of the various techniques which were employed have yet been elucidated satisfactorily. Kok, from this laboratory, recently has reviewed the field in great detail (17). The above studies represent investigations on the photosynthetic efficiency in its strictest sense. On the other hand there are investigations of a different type but of equal interest, viz., on the efficiency of the outcome of photosynthesis in the long run such as the efficiency of growth, extending from small algal cultures in the laboratory, under controlled conditions, via algal mass cultures, both in the laboratory and in open air, to efficiency of energy conversion in field crops, and ultimately to speculations about the world energy yield on the land and in the oceans.

In our laboratory, we have been working on this type of problem for several years and thus it seems appropriate to survey a few results of the various aspects in this article. The more so, since the great shock of Robert Emerson's sad and unexpected death by itself led us to reflect upon the diverse aspects of the field in which he was deeply interested (6).

The work in our laboratory was initiated after the last world war by calculations of maximal efficiencies for some field crops, taking high annual yields in Holland, from agricultural data, making allowance for roots, stubbles, etc., and comparing them with the average energy on the cultivated surface during the growth period (27). Considering only wave lengths available for photosynthesis, the efficiencies were between 0.5 and 2 %, and the large deviation from photosynthetic efficiency in laboratory experiments of short duration—viz., 20 to 30 %—was the starting point of our work. Earlier computations of efficiency of higher plant growth are discussed in detail in (11). The possible reasons for the relatively low long term efficiency are as follows (27): 1) too high incident light intensities under field conditions; 2) too low CO_2 content of the air; 3) too low temperatures; 4) other limiting factors, e.g., too little water; 5) loss of light between the plants; and 6) factors, provisionally difficult for analysis, e.g., fluctuating rate of photosynthesis, possible "afternoon depression," respiratory losses.

It was stated that several of these factors could be controlled more easily in algal cultures than in the growth of field crops.

EFFICIENCY OF ALGAL GROWTH: The first question to be answered was whether the efficiency of growth, under favorable conditions, could approach closely that of photosynthesis short-term experiments. Work along this line was started in our laboratory in June 1948 by Miss J. T. de Vries, and extended by J. F. Bierhuizen in 1949 using about 0.5 liter Chlorella cultures illuminated by incandescent lights under laboratory conditions, (details in (28)). Over the period of active growth the efficiency of light energy conversion ranged from 12 to 15 % at relatively high light intensities, and from 20 to 24 % at lower light intensities. Thus, it appeared that, under suitable conditions, the efficiency of growth in algal cultures did approach closely that of short-term photosynthesis, being about 25 % (assuming a quantum yield of approximately 0.1). Shortly thereafter, Kok established complete energy balances of algal cultures, cultivated in large Warburg manometer vessels, in sodium light. In Kok's studies all relevant items were measured (12). They confirmed the preliminary data discussed above.

Large scale (300 l) indoor and outdoor mass cultures of algae were set up first in 1950–51 chiefly by van Oorschot. These gave high efficiencies under laboratory conditions, at relatively low light intensities, and high temperatures. A series of 9 experiments gave an average efficiency of 13.3 %, with a maximum of 19.7 %. Outdoor cultures in full daylight showed a much lower yield, viz., 2.6 %, which could be increased to 6.3 % by the application of gauze screens, which reduced the light intensity (19, 28).

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A more detailed analysis, using much smaller vessels, showed that under conditions of full summer daylight efficiencies of the order of 8 % were obtained (18). This corresponds to a yield of about 20 g dry weight/m²/day. Similar yields also have been obtained in other laboratories (survey in (24)).

In all our cultures, CO_2-enriched air was applied. After 1954 interest concentrated on several problems that had arisen from previous work: intermittency and high light intensity effects on the photosynthetic apparatus, including spectral changes (13, 14, 15, 16), and the relation between the carbon and nitrogen metabolism of Chlorella (1, 2). With respect to our present discussion, it is of interest that algae growing with a relatively low supply of nitrogen first accumulate carbohydrates, and finally fats, with a continuous decrease in the efficiency of light energy conversion (1, 19).

Recently, we were able to devote renewed attention to the mass culture aspect as such, in relation to efficiency. Previous work had shown that the type of culture vessel was important in obtaining high efficiencies, this effect still is not fully understood. In our recent approach we adopted a technical solution to the stirring problem by introducing washing machines as culture vessels. The type used had a cylindrical transparent lucite container, ("demonstration" model) about 50 cm diameter and 30 cm high (manufacturer: Miele). These provided excellent algal growth. Preliminary series run in the summer of 1958 gave yields of 13 to 22 g dry weight/m²/day, the average efficiencies of the series were from 4.7 to 7.2 %, with daily extremes between 2.0 and 10.5 %. This culture device was very suitable for additional heating, CO_2-supply, and for renewal of part of the suspension. It seems probable that the yields so far obtained may be increased considerably as we learn to improve the composition of the culture solutions and the other conditions. In addition, we are also experimenting with some continuous culture devices which, however, are on a smaller scale. (E. C. Wassink and C. Kaai, to be published).

EFFICIENCY OF HIGHER PLANT GROWTH: Along with this algal work, we have been interested in the efficiency of solar energy conversion in field crops.

Close to the large scale outdoor Chlorella cultures, a grass area of 1 m² in an existing lawn was treated as an experimental plot. Three successive harvests between May and the end of October gave an average efficiency of 2.6 % of the incident, photosynthesizible radiation (28).

Beet seedlings raised in this laboratory by Glas and Gaastra, in 1949, under artificial light of rate-limiting intensities, showed efficiencies of 12 to 19 % (28). More recent experiments under optimal conditions and complete leaf cover of the soil surface gave about the same values; in younger stages the yields were lower (9 to 11 %). Similar experiments in the laboratory under light limiting conditions, using other plants, (turnip and cucumber etc.) showed efficiencies mostly between 7 and 11 %.

Gaastra (7), measured directly the efficiency of photosynthesis of sugar beet leaves under mercury light, with the aid of an infra-red gas analyzer and, by inference, calculated the efficiency in full summer sunlight. The (maximum) efficiency at low light intensities was about 17.8 % (referring to incident light), and about 2 % at full sunlight intensity. At an intensity of 10^4 ergs/cm² sec the rate of photosynthesis was 26 cmm CO_2 per hour per cm² leaf surface which, for high pressure mercury light amounts to a quantum yield of 0.10, confirming earlier observations for leaves which showed maximum values mostly between 0.05 and 0.10 (8, 26).

The annual efficiency of a good beet crop is around 2.2 % (27). Gaastra (7) was the first to point out that this does not necessarily mean that the yield is the same over the entire season. Obviously, the yield cannot be constant, since, in the beginning, the field is scarcely covered while, toward the end, the growth rate slows down considerably. Combining data from growth experiments on sugar beets, performed at Wageningen by Boonstra (3) with corresponding solar energy data (31), Gaastra showed that the efficiency had a maximum of 7 to 9 % in the middle of the season and that between 80 and 90 % of the total organic matter was produced in 45 % of the season (or 2.5 months). This efficiency may be compared with the best values obtained with algae.

Between 1949 and 1951 we carried out a periodic harvest experiment with potatoes in order to establish the trend of the efficiency values. Recently, all the relevant energy data have been worked up. The efficiencies, calculated for surface area actually covered, showed some increase during the 1st half of the season; optimal efficiencies were of the order of 5 %. A more detailed discussion of this experiment is planned elsewhere (30).

In the summer seasons of 1957 and 58, Kamel, in this laboratory, made an elaborate study of growth and efficiency in barley, under natural conditions, employing 4 different light intensities (by artificial shading), and, in separate experiments, 3 different plant densities. The efficiency showed a trend with time similar to the one evaluated for beets by Gaastra (7), being most pronounced at full light intensity. At lower intensities the seasonal efficiency curve was flattened, and the growing period was extended. In the density series, the efficiency curves are all more nearly equal. At first it may seem remarkable that the efficiency of solar energy conversion was highest at the highest light intensity, both in the middle of the season and overall, however, early and late in the season the efficiency declined sharply. The maximum efficiency recorded (on the basis of area actually covered) was about 13.5 % for a period of about 2 weeks in the middle of the season, followed by a sharp decrease. The average efficiency (per cultivated area) over the entire season was 2.9 % for full daylight, and 1.4 % for the lowest light intensity, viz., 25 % of full daylight. The total dry weight per plant in 25 % of full daylight is only about 15 % of that under full light. Apart from unfavorable morphogenetic reactions at the low light intensity, the integration of slower growth over a long period of time and the, presumed, relatively less positive daily energy balance may tentatively explain these figures. For more details we refer to the original papers (10, 11). Also with sugar beet similar, however, less extensive experiments have been carried out (10, 11).

Efficiency of Plant Growth on Earth and its Utilization by Man: Unpublished calculations for efficiency of tree growth in temperate regions on the basis of literature data, carried out by the author showed about the same efficiency values as obtained for field crops, viz. 1 to 2 % of photosynthesizible radiation during the growing season.

Rabinowitch has estimated that per annum about 2.5×10^{23} cal photosynthesizible radiation reaches the earth surface, and that 3×10^{21} cal is fixed by photosynthesis (20, p. 9), so that the overall efficiency is about 1.2 %, including land and oceans. Since 1 ton of carbon is equivalent to about 10^{10} cal, this corresponds to 3×10^{11} tons of carbon. An estimate from certain actual data yields about 1.75×10^{11} tons (20, p. 7). From this figure about 80 % is attributed to the oceans.

For the land area, the estimate is 0.19×10^{11} tons of carbon fixed per annum, which was derived from Schröder's computation (21). This figure may be checked as follows: The wooded area on earth is about 40×10^6 sq km (44×10^6 sq km according to Schröder (21), 36.5×10^6 sq km according to more recent data (25)). Using the data quoted in the 1st paragraph of this section, and assuming that the average production of forests is well reflected by that of temperate regions, the annual yield of a wooded area may be estimated to 10000 kg dry matter per hectare = 10^6 kg per sq km (see also (27)). This would correspond to a carbon yield of 0.4×10^6 kg, or of $36.5 \times 10^6 \times 0.4 \times 10^6 = 1.45 \times 10^{13}$ kg or 0.15×10^{11} tons for the total. The total carbon fixation on the total land area, according to Schröder, is about 1.5 times that of the woods alone, it covers about 150×10^6 sq km. However, about 80 x 10^6 sq km are areas of low plant production (arid and semiarid regions). This would, altogether, yield a figure slightly higher than 0.2×10^{11} tons, in very close agreement with Schröder's estimate. Of this total, about one third or 0.07×10^{11} tons might be chiefly agricultural crops, whose cultivated area is about 27×10^6 sq km (21).

The world's human population may be estimated to consume $2.5 \times 10^9 \times 365 \times 2 \times 10^3$ kcal per annum, or 2×10^{15} kcal, in which the average personal daily consumption is set at 2×10^3 kcal.

Stamp (22) has estimated that world's average need for human food is about 10^6 kcal per individual per annum, yielding a slightly higher total figure.

According to our estimations, the annual caloric production of the arable land is about 7×10^{16} kcal, so that the fraction now used for food is about 0.03 or 3 %, and 3×10^{-4} of the solar radiation, assuming a photosynthetic efficiency of 1 %. Thus, the solar radiation in question would amount to 7×10^{18} kcal. In reality, the area outside the woods covers about 60 % of the land area. The land area is about 0.3 of the total earth surface and thus receives about 8×10^{19} kcal of photosynthesizable radiation; 60 % being 5×10^{19} kcal. The average efficiency of photosynthesis outside the woods thus is $7/5 \times 10^{-1} \times 1\ \% = 0.14\ \%$. One might say that the "effective cross section" for photosynthesis of the land area outside the woods is 0.14, taking 1 % as a fair average for photosynthesis under natural conditions during the period of growth. Following Schröder's estimation and dividing the land into units of 10^6 sq km, the land area is roughly composed of 40 units of wood, 30 of farmland, 30 of semi-arid land and 50 of arid land. The actual efficiency of the farmland region—assuming that this produces the bulk of the above crop yield—thus would be $110/30 \times 0.14 = 0.5\ \%$. The same holds, by inference, for the wooded area, and is based on our assumption of 10000 kg per ha average annual production which received support from Schröder's data. Assuming an average growth efficiency of 1 % over large areas, including lost surfaces like rivers, etc. it would mean that the average growing season is 0.5 year which seems reasonable.

We still make the relation: human consumption to photosynthesizable solar energy received. For the total land area, this is $2 \times 10^{15}/8 \times 10^{19} = 0.25 \times 10^{-4}$. It should be mentioned that, according to Stamp (22) only about 30 % of the land area is habitable by man, 20 % being too cold, 20 % too dry, 20 % too mountainous, and 10 % rocky and soilless. According to this estimate, the wood area must be largely outside the potentially habitable area which can be true only in part. Taking Stamp's data, the total human consumption would be equivalent to about 10^{-4} of the solar radiation on this area and probably about twice as high (2×10^{-4}) if wood consumption is included since forests for a considerable part belong to the potentially habitable area.

It is interesting to compare this figure with an estimate for the Netherlands as a country distinguished by a number of interesting peculiarities, viz., 1) the population density has essentially reached a "habitable" upper limit, 2) it has very little area which is in principle unhabitable 3) it is using almost completely any recreation areas and has very few true nature reserves. The area is roughly 3.10^4 sq km, the number of inhabitants 1.1×10^7. Photosynthesizable solar energy per annum is about 3.7×10^{11} kcal per sq km, in total thus 1.1×10^{16} kcal. The amount of food consumed (ca. 3000 kcal/day) is $3.65 \times 10^2 \times 3 \times 10^3 \times 1.1 \times 10^7 = 1.2 \times 10^{13}$ kcal, or 10^{-3} of the photosynthesizible radiation.

If we take the situation in the Netherlands as a rather uncomfortable and nearly impossible situation for Stamp's habitable world area as a whole, this area, on the average, is already at 20 % of this limit (For these considerations it is not very relevant if some food is imported or exported.) According to Daniel's figures (4) in the U.S.A. the average use of food is only 10^{-5} of incident solar radiation on the entire surface and about 10^{-4} of the radiation on Stamp's inhabitable area, which is near the world average.

The figure about the Netherlands is also interesting because it shows that a dense population has no more food at its disposal than about 0.1 to 0.2 of the potential photosynthetic production on the entire area and, in addition, probably a similar amount of wood. It is easily understandable that this figure is low for several reasons, e.g., 1) areas taken up by roads and social constructions, 2) areas taken by rivers, 3) only part of the crop is food, 4) necessary wood and recreation areas.

This figure for the Netherlands may have an absolute meaning since both agricultural yields per unit area and relative size of arable land are at a maximum. Only food production during the entire year by a more efficient principle (e.g., by very efficient algal cultures) might improve the situation materially. One word may be said about air pollution brought about by a dense population living according to contemporary standards. In the Netherlands, higher plants in general do not yet seem to suffer seriously from air pollution. It may be remarked, however, that lichens, known to be particularly sensitive in this respect, have practically disappeared during the last 30 years.

In the twenties the more conspicuous species, e.g. of the genera Usnea, Ramalina, Evernia and Parmelia, were still also very common in the immediate neighborhood of the smaller cities and villages, whereas now they are not seen any more even in the countryside. There is no scientific proof that this is (only) due to air pollution, but it seems very probable that this is the main reason, and well deserves attention. Apart from the decline in beauty and interest, the loss of the lichens may well mark a first step on a dangerous road, along which other types of organisms also may travel sooner or later.

The number of human beings on earth has increased rapidly during the last century. In the Netherlands there is 1 inhabitant on each 0.3 ha., the world average is 1 on 5 ha. (according to Stamp (22)). It is difficult to say what would be the relation if man still lived as a normal constituent of natural biotypes, like animals do. The primitive civilizations that still exist already have a long human history, and their distance from a truly primitive state is probably larger than that between our present civilization and theirs. However, for our problem, they may serve as a basis for comparison. Thus, e.g., in New Guinea around 1940 1.3×10^6 inhabitants lived on 8×10^7 ha, or 1 on 60 ha, in contrast to Java where it was 1 on 0.3 ha. The New Guinea figure is very low, especially in view of the fact that the greater part of the country may be habitable according to Stamp's considerations. About the same figure holds at present for Canada (22), which, may be for different reasons, however, as a large part of the country may be too cold for permanent habitation.

The figure for the U.S.A. is about the world average (22), which is roughly 10 times larger than the New Guinea figure, and about 10 times smaller than the figure for the Netherlands. It should be observed that the U.S.A. has a large inhabitable area. It is interesting that the increase in population up to this level in the U.S.A. has already entailed the loss of most of the virgin aspects of nature (c.f. e.g., the disappearance of the prairie type of vegetation, and also of the virgin forests (9)).

The above considerations primarily dealt with a consideration of plant growth on land. We will now consider briefly the oceans. Schröder had estimated the production of the ocean to be about the same total as that of the land (the oceans are roughly 3.5×10^8 sq km against 1.5×10^8 sq km for the land; the yield per unit area thus would be about 3/7 that of the land). Rabinowitch (20) quotes a much higher figure, viz., about 1.6×10^{11} tons against 0.2×10^{11} tons for the land area. This figure was mainly based upon Riley's data; it corresponds to about 0.9 % efficiency of solar energy conversion for the entire ocean area during the whole year.

More recently, Steemann Nielsen (23) arrived again at a much lower figure, viz. 55 g C/m^2 per annum. This would amount to a total of 0.2×10^{11} tons, almost exactly as Schröder had estimated; it would bring down the average efficiency of solar energy conversion to about 0.11 % for the whole year for the entire ocean area. The average efficiency for the entire land area is about 0.27 %, according to our preceding computations, for the whole year.

It would seem more satisfactory that the yield of the ocean per unit surface area comes out less than that of the land since, on the average, the ocean is definitely less green than the land. This is not compensated by the thick layer of water in which organism may live, for looking from the surface, it would have to give a densely green (or brown) impression in order to give a high yield.

We can estimate, therefore, that the world production of plant material is around $2 \times 0.2 \times 10^{11}$ or 0.4×10^{11} ton C per annum, equivalent to 0.4×10^{18} kcal, or about 1/7 of Rabinowitch's estimate, viz. 3×10^{18} kcal. The average efficiency of solar energy conversion on the entire earth surface thus would amount to 1/7 of the Rabinowitch figure, viz. $1/7 \times 1.2 = \sim 0.17$ %.

The resources man derives from the sea are estimated between 0.5 and 1 kg/ha per annum. This is excessively low as compared with the land which yields roughly 2 ton C per sq km or 50 kg dry CH_2O per ha. The 0.5 to 1 kg for the ocean may correspond to $\sim$0.1 kg dry weight, or $\sim$500 times less than the profit of land vegetation.

I have previously tried to estimate the entire production of the sea from average fish catches (28), assuming that 1 kg of fish is derived ultimately from 25 kg of phytoplankton, that 1 % of all fish is caught, and that 1 % of the living matter in the ocean is fish. This yields an annual production of 2.5×10^4 kg dry matter or 10^4 kg C per ha per annum, or 10^6 kg C per sq km. For the entire area of the ocean this would be $3.5 \times 10^8 \times 10^6 = 3.5 \times 10^{14}$ kg C per annum, or 3.5×10^{11} ton. This would double the Rabinowitch figure for the oceans, which seems very improbable. However the assumptions employed were only approximations. Perhaps much more than 1 % of all fish are caught, or possibly much more than 1 % of all living matter in the ocean is fish. It would be worth while to assemble data with respect to these assumptions which would help us to substantiate further the recent estimates on photosynthesis in the oceans, and thus on the total yield of plant growth on earth.

The discussion in the last section may serve as a preliminary approach to the problems outlined. A full evaluation will require a thorough comparison and consideration of detailed data on the various fields of production, and on climatic influences, which is beyond the scope of this article. Moreover, detailed analyses should first be extended in various directions. It is hoped, however, that the order of magnitude of the computed values is correct.

Summary

Algal growth, in principle, may constitute a very efficient source of solar energy conversion. Also in large cultures, efficiencies of 7 to 10 % with regard to the photosynthesizible part of full intensity solar radiation have been obtained.

Higher plant growth, in principle, is no less efficient, but during part of the season while inefficient periods are necessarily included. The overall yield during a season mostly lies between 1 and 2 %.

Weakening of the light intensity may result in an increase in efficiency, other conditions permitting.

Estimations of yield and efficiency of solar energy conversion by plant growth on the entire earth have been discussed, as well as some relations with its use by man. The most probable figure for the yield of plant growth on earth appears to be around 0.4×10^{11} tons of carbon per annum, half of which is produced on the land, and half in the oceans. The average efficiency of conversion of photosynthesizable radiation is around 0.17 %, that of the land area $\sim$ 0.27 %, and that of the ocean $\sim$ 0.11 %. Density of human population is unlikely to be able to increase beyond utilization for nutrition of $\sim$ 0.1 % of photosynthesizable radiation on the habitable land area.

Literature Cited

1. Bongers, L. H. J. Aspects of nitrogen assimilation by cultures of green algae. Mededel. Landbouwhogeschool Wageningen. 56(15): 1–52. 1956.
2. Bongers, L. H. J. Kinetic aspects of nitrate reduction. Netherl. Journal of Agricultural Science 6: 79–88. 1958.
3. Boonstra, A. E. H. R. Rasverschillen bij bieten, VI: Mededel. Inst. Suikerbietenteelt 12: 13–95. 1942.
4. Daniels, F. Solar energy. Science 109: 51–57. 1949.
5. Emerson, R. and Lewis, C. M. Factors influencing the efficiency of photosynthesis. Amer. Jour. Bot. 26: 808–822. 1939.
6. Emerson, R. The quantum yield of photosynthesis. Ann. Rev. Plant Physiol. 9: 1–24. 1958.
7. Gaastra, P. Light energy conversion in field crops in comparison with the photosynthetic efficiency under laboratory conditions. Mededel. Landbouwhogeschool Wageningen 58(4): 1–12. 1958.
8. Gabrielsen, E. K. Quantum efficiency in photosynthesis. Experientia 3: 439–442. 1947.
9. Gaffron, H. Photosynthesis and the production of organic matter on earth. In: Currents in Biochemical Research, D. E. Green, ed. Pp 25–48. Interscience, New York 1946.
10. Kamel, M. S. Efficiency of solar energy conversion as related with growth in barley. Mededel. Landbouwhogeschool Wageningen 58(8): 1–19. 1958.
11. Kamel, M. S. A physiological study of shading and density effects on the growth and the efficiency of solar energy conversion in some field crops. Mededel. Landbouwhogeschool Wageningen 59(5): 1–102. 1959. (In press.)
12. Kok, B. On the yield of Chlorella growth. Acta Bot. Néerl. 1: 445–467. 1952.
13. Kok, B. Photosynthesis in flashing light. Biochim. Biophys. Acta 21: 245–258. 1956.
14. Kok, B. On the inhibition of photosynthesis by intense light. Biochim. Biophys. Acta 21: 234–244. 1956.
15. Kok, B. On a reversible absorption change at 705 mμ in photosynthetic organisms. Biochim. Biophys. Acta 22: 399–401. 1956.
16. Kok, B. Changes of absorption spectrum induced by illumination, and their bearing on the nature of the photoreceptor of photosynthesis. Proc. of the 2nd International Congress of Photobiology, Torino. Pp. 369–383. 1957.
17. Kok, B. Efficiency of photosynthesis. In: Encyclopedia of Plant Physiology, Vol. 5. Springer, Berlin, Göttingen, Heidelberg (In press.)
18. Kok, B. and van Oorschot, J. L. P. Improved yields in algal mass cultures. Acta Botan. Néerl. 3: 533–546. 1954.
19. Oorschot, J. L. P. van. Conversion of light energy in algal culture. Mededel. Landbouwhogeschool Wageningen 55: 225–276. 1955.
20. Rabinowitch, E. I. Photosynthesis Vol. 1. Interscience, New York 1945.
21. Schröder, H. Die jährliche Gesamtproduktion der grünen Pflanzendecke der Erde. Naturwiss. 7: 8–29. 1919.
22. Stamp, L. D. The measurement of land resources. Geograph. Rev. 48: 1–15. 1958.
23. Steemann Nielsen, E. Light and the organic production in the sea. In: Measurements of Primary Production in the Sea. International council for the Exploration of the Sea. Symposium 1957, Paper No. 2.
24. Tamiya, H. Mass culture of algae. Ann. Rev. Plant Physiol. 8: 309–334. 1957.
25. Vries, E. de. De aarde betaalt. Albani, The Hague (Neth.), 1948.
26. Wassink, E. C. Experiments on photosynthesis of horticultural plants with the aid of the Warburg method. Enzymologia 12: 33–55. 1946.

27. WASSINK, E. C. De lichtfactor in de photosynthese en zijn relatie tot andere milieufactoren. Med. Dir. v.d. Tuinbouw 11: 503–513. 1948.

28. WASSINK, E. C., KOK, B. and OORSCHOT, J. L. P. VAN. On the yield of light energy conversion in Chlorella cultures as compared with higher plants: In: Algal Culture from Laboratory to Pilot Plant, J. S. Burlew, ed. Pp. 55–62. Carnegie Inst. of Washington. Publ. 600. 1953.

29. WASSINK, E. C. Problems in the mass cultivation of photo-autotrophic micro-organisms. In: Autotrophic Micro-organisms. Pp. 247–270. University Press, Cambridge 1954.

30. WASSINK, E. C. Efficiency of solar energy conversion in field crops. To be presented at 9th Intern. Botanical Congress, Montreal, Canada, Aug. 1959. (Summary in press.)

31. ZUIDHOF, G. and VRIES, D. A. DE. Stralingsmetingen te Wageningen 1930–1940. Mededel. Landbouwhogeschool Wageningen 44(5): 1–8. 1940.